

Retention of dormant copepods in deep basins of the Southern California Bight

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ABSTRACT: The vertical distribution and abundance of dormant *Calanus pacificus* were described in deep basins and at deep, non-basin locations in waters off Southern California in October 1999 and 2000 and January 1999. Dormant *C. pacificus* were present in deep water at all stations sampled. In each month, vertical distributions were similar across the region sampled. The abundance of dormant *C. pacificus* was higher and their depth range was broader and deeper in October than in January. There was no difference in the abundance of dormant *C. pacificus* in basins and at deep, non-basin locations in October. Except for the Santa Barbara Basin, Southern California Bight basins were too deep relative to the vertical distribution of dormant *C. pacificus* to trap dormant copepods. Migration to deep water during dormancy in this region removes copepods from equatorward flow in surface waters. Dormant copepods are exposed either to poleward flow at the shallow end of their depth range in the continental borderlands of Southern California, or to very low current velocities in deeper water, both at basin and non-basin locations. The broad horizontal distribution of dormant *C. pacificus* in this region implies that non-point sources are dominant in re-seeding surface waters at the end of the dormant season.

KEY WORDS: *Calanus pacificus* · California Current · Copepod · Diapause · Dormancy · Retention

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INTRODUCTION

The life cycle of the dominant California Current copepod species *Calanus pacificus* includes a period of dormancy and descent to deep water that allows copepods to escape from seasonally unfavorable conditions at the surface (Alldredge et al. 1984, Osgood & Frost 1994, Dahms 1995, Osgood & Checkley 1997a,b, Ohman et al. 1998). Dormancy is a state of suppressed development, often occurring in the fifth copepodid (C5) stage of development in oceanic copepods and associated with cessation of feeding, reduced metabolic rates, high lipid reserves, resistance to anaerobiosis, and inactivity (Hirche 1996). In eastern boundary current systems, as in other ocean regions where surface advection is strong, transport out of productive regions may have a significant influence on copepod

populations (Peterson 1998). Descent to deep water during dormancy can alter the flow regime to which copepods are exposed and influence horizontal transport, potentially increasing retention in favorable regions (Eiane et al. 1998).

Copepod transport and retention during dormancy can be influenced by bathymetry, for example when copepods migrate below the sill depth of continental shelf basins or fjords (Sameoto & Herman 1990, Osgood & Frost 1996). Basins and fjords, where deep water is bathymetrically isolated and mean current velocities are near zero, may act to aggregate and retain dormant copepods, if copepods descend from water advected over the basin (Sameoto & Herman 1990, Osgood & Checkley 1997b, Bagøien et al. 2000). High concentrations of dormant C5s in the Santa Barbara Basin, at the northern end of the Southern Cali-

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fornia Bight (SCB; Fig. 1), have been attributed to retention of individuals advected over the basin during the onset of dormancy and migration to deep water (Alldredge et al. 1984, Osgood & Checkley 1997a,b). These locations may serve as point sources of copepods seeding surface waters when they emerge from dormancy. Alternatively, descent to deep water in areas where subsurface flow is in opposition to surface flow, such as poleward undercurrents in eastern boundary current systems, may transport copepods back to productive regions (Fleminger 1966, John et al. 1998, Peterson 1998, Johnson & Checkley 2004). This process may serve as a non-point source of individuals reseeding surface waters at the end of the dormant period. Dormant *Calanus pacificus* may be influenced both by retention in basins and transport in the undercurrent. High concentrations of dormant *C. pacificus* have been observed in the Santa Barbara Basin (Alldredge et al. 1984, Osgood & Checkley 1997a,b). Lower concentrations have been observed in the water column outside of basins, at the depth of the undercurrent, and in deeper water (Longhurst 1967, Ohman et al. 1998, Johnson & Checkley 2004).

The SCB (Fig. 1) is a bathymetrically complex region of basins and ridges bounded by the coast from Point

Conception, USA, to Cabo Colnett, Baja California, Mexico, and by the Santa Rosa–Cortez Ridge to the west. Seven of the submarine basins in the SCB, including the Santa Barbara Basin, are north of the United States–Mexico border (Emery 1960). The California Undercurrent, which is warmer, saltier, and lower in oxygen than the equatorward California Current, flows poleward along the continental slope into the SCB. California Undercurrent flow is influenced by the complex bathymetry of the SCB, which steers the core of the undercurrent westward to the south of the Channel Islands and other branches through gaps in the Santa-Rosa–Cortez Ridge and through the Anacapa Passage (Lynn & Simpson 1990).

The objective of the present study was to determine whether dormant copepods are aggregated and retained in basins of the SCB. The distribution and abundance of *Calanus pacificus* C5s emerging from dormancy, as well as the timing of emergence, set initial conditions for population growth of open-ocean copepods during favorable periods. If basins aggregate and retain dormant copepods, then these locations could serve as point sources of copepods seeding surface waters when they emerge from dormancy. Thus, interactions between dormancy behavior and

local bathymetry could impose spatial structure on the initial conditions for population growth. Understanding these interactions is essential to modeling copepod population dynamics and predicting their response to climate variability.

MATERIALS AND METHODS

Vertically stratified zooplankton samples were collected at 10 stations in October 1999 and 2000 and at 13 stations in January 1999 (Table 1, Fig. 1), as seasonally maximal abundances of dormant *Calanus pacificus* had been observed in October or November (Osgood & Checkley 1997b, Johnson & Checkley 2004). Samples were collected using a 1 m², 10 net MOCNESS, equipped with 333 µm mesh nets and pressure, conductivity, temperature, and dissolved oxygen sensors. Sampling was performed during California Cooperative Oceanic Fisheries Investigations (CalCOFI) quarterly monitoring cruises, and tows were performed as stations were encountered (for times, see Table 1). Basins chosen for sam-

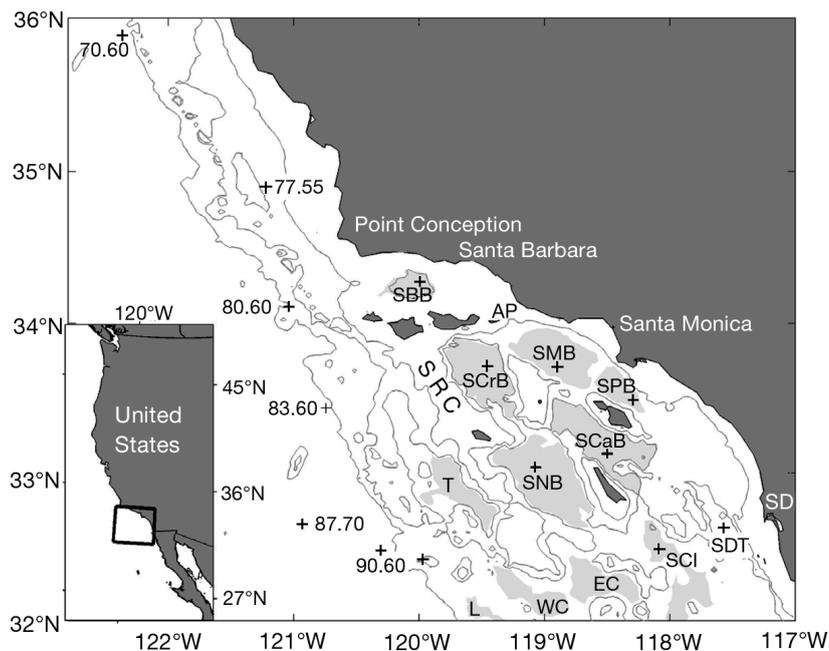


Fig. 1. Southern California Bight and station locations (+: MOCNESS starting locations; AP: Anacapa Passage; SD: San Diego; SRC: Santa Rosa–Cortez Ridge). Depths are in meters. Basins sampled were Santa Barbara Basin (SBB), Santa Monica Basin (SMB), Santa Cruz Basin (SCrB), San Nicholas Basin (SNB), Santa Catalina Basin (SCaB), and San Clemente Basin (SCI). Open water stations sampled included San Diego Trough (SDT) and numbered California Cooperative Oceanic Fisheries Investigations (CalCOFI) stations. Un-sampled basins in the region shown are East Cortez Basin (EB), Long Basin (L), San Pedro Basin (SPB), Tanner Basin (T), and West Cortez Basin (WC)

Table 1. Sampling dates and positions (in degrees and minutes). Numerical station designations are in CalCOFI format (i.e. line number.station number). Starting positions of stations marked with an asterisk deviated from the CalCOFI station position

Station	Date	Time-start (h)	Lat. (N)	Long. (W)
Santa Barbara Basin	28 Jan 1999	02:20	34°16.1'	119°59.3'
Santa Monica Basin	16 Jan 1999	21:16	33°41.6'	118°52.5'
San Pedro Basin	15 Jan 1999	22:36	33°29.8'	118°17.5'
Santa Catalina Basin	15 Jan 1999	06:06	33°09.2'	118°34.5'
Santa Cruz Basin	28 Jan 1999	19:31	33°42.1'	199°30.1'
San Nicolas Basin	14 Jan 1999	22:40	33°05.4'	119°01.9'
San Clemente Basin	29 Jan 1999	09:37	32°29.1'	118°05.1'
70.60	27 Jan 1999	04:40	35°53.2'	122°21.9'
77.55	24 Jan 1999	16:03	34°54.0'	121°13.2'
80.60	27 Jan 1999	17:48	34°09.1'	121°09.0'
83.60	28 Jan 1999	10:38	33°34.8'	120°45.4'
87.70	18 Jan 1999	01:57	32°40.5'	121°03.8'
90.60	14 Jan 1999	05:40	32°25.3'	119°57.9'
Santa Barbara Basin	15 Oct 1999	13:42	34°16.6'	119°59.6'
Santa Monica Basin	10 Oct 1999	01:16	33°42.7'	118°53.7'
Santa Catalina Basin	20 Oct 1999	17:03	33°08.0'	118°30.0'
Santa Cruz Basin	14 Oct 1999	23:34	33°43.1'	119°27.5'
San Nicolas Basin	20 Oct 1999	10:38	33°02.5'	119°04.4'
80.60	16 Oct 1999	04:44	34°06.7'	121°02.5'
83.60	14 Oct 1999	04:40	33°26.1'	120°44.6'
87.70	11 Oct 1999	04:59	32°39.4'	120°55.8'
90.60*	19 Oct 1999	21:33	32°28.8'	120°18.3'
San Diego Trough	21 Oct 1999	02:50	32°37.9'	117°34.4'
Santa Barbara Basin	26 Oct 2000	05:04	34°16.3'	120°00.1'
Santa Monica Basin	19 Oct 2000	21:17	33°41.6'	118°52.8'
Santa Catalina Basin	18 Oct 2000	13:15	33°09.6'	118°34.8'
Santa Cruz Basin	25 Oct 2000	13:47	33°44.2'	119°29.7'
San Nicolas Basin	31 Oct 2000	00:42	33°01.1'	119°03.7'
80.60	26 Oct 2000	22:45	34°09.1'	121°09.4'
83.60	24 Oct 2000	22:41	33°35.3'	120°47.8'
87.70	21 Oct 2000	01:45	32°39.5'	121°07.1'
87.70	30 Oct 2000	11:29	32°39.8'	121°02.8'
90.60*	17 Oct 2000	14:37	32°22.1'	120°12.1'
San Diego Trough	12, 13 Oct 2000	22:48 and 02:42	32°37.5'	117°31.0'
San Diego Trough	31 Oct 2000	12:48 and 16:17	32°37.0'	117°31.5'

pling represent a range of bottom and sill depths (Table 2). They were sampled from the surface to 50 m above the bottom, except at the Santa Barbara Basin, which was sampled to 15 m above the bottom (depth strata sampled replicated Osgood & Checkley 1997a,b). The non-basin stations chosen for sampling, except the San Diego Trough, were CalCOFI grid stations and are identified by their CalCOFI station numbers (i.e. line number.station number). The starting position of Station (Stn) 90.60 was shifted northwest from its CalCOFI grid location in October of 1999 and 2000, due to shallow bathymetry at CalCOFI Stn 90.60. Non-basin stations were sampled from the surface to either 2000 or 50 m above the bottom. However, Stn 80.60 was sampled to 1000 m only, due to the proximity of a seamount to the towing track. In October 2000, the San Diego Trough was sampled on 2 dates, and vertical profiles of copepod abundance were concate-

nated from 2 tows on each date (Johnson & Checkley 2004). The abundance estimate at the San Diego Trough in October 2000 was a mean of the 2 dates sampled. The vertical profile of copepod abundance at Stn 87.70 was concatenated from tows on 2 dates in October 2000 (Table 1).

Samples were quantitatively split after collection using a Folsom splitter, and half was preserved in borate-buffered, 5% formalin. The abundances of male and female adult (C6) stages, C5s, and fourth copepodid (C4) stages were estimated by enumerating sub-samples of formalin-preserved zooplankton samples. Vertical distributions of dormant C5s were characterized as an estimated median depth, i.e. the mid-depth of the net stratum including the median depth, and a semi-quartile range, i.e. the distance between the median depths of net strata including the first and third depth quartiles. This estimate was subject to high uncertainty associated with the depth stratum size. A 2-way analysis of variance was used to test whether the abundance of dormant C5s was different in basin and non-basin stations and in the 2 yr sampled, and whether there were interactions between sampling year and station type. Student's *t*-tests on arcsine-transformed data were used to test whether the relative abundance of C5s was different in January versus October.

To identify water mass affiliations of dormant copepods, California Current and California Undercurrent waters were differentiated by their characteristic combinations of temperature and salinity, which are higher at a given density in the undercurrent, reflecting its equatorial source (Lynn & Simpson 1990). Methods are described in detail in Johnson & Checkley (2004).

RESULTS

The dominant developmental stage of *Calanus pacificus* observed in October of 1999 and 2000 was C5 (85 ± 21 and 94 ± 8% of total C4 to C6 abundance; $\bar{x} \pm$ SD). They were present both at the surface and in deep water at all stations sampled in October in both years (Fig. 2). Although the vertical resolution of sam-

Table 2. Bottom depth at MOCNESS starting positions and basin statistics (Emery 1960)

Station	Bottom depth (m)	Max. basin depth (m)	Sill depth (m)	Basin volume (km ⁻³)
Santa Barbara Basin	577	627	475	46
Santa Monica Basin	910	938	737	208
San Pedro Basin	890	912	737	79
Santa Catalina Basin	1290	1357	982	429
Santa Cruz Basin	1930	1966	1084	875
San Nicolas Basin	1757	1832	1106	962
San Clemente Basin	1934	2107	1816	121
CalCOFI 70.60	3080			
CalCOFI 77.55	570			
CalCOFI 80.60	2300			
CalCOFI 83.60	1389			
CalCOFI 87.70	3600			
CalCOFI 90.60	1040			
San Diego Trough	1180			

2000: $3.1 \pm 4.4\%$; $\bar{x} \pm SD$; Fig. 3). Fourth copepodids and adults were observed mainly in the upper 200 m, and C5s were overwhelmingly dominant below 200 m (99.4 \pm 0.6% of individuals below 200 m in 1999; 99.8 \pm 0.3% in 2000; $\bar{x} \pm SD$). Dormancy in deep-dwelling C5s was inferred here based on their dominance in deep water. The dominance of post-molt jaw phases among deep-dwelling C5 stages at the San Diego Trough station in October 2000 (Johnson 2004) supports this interpretation. C5s below 200 m will hereafter be referred to as 'dormant' or 'deep-dwelling.'

Dormant copepods occupied a broad depth range, extending to the deepest strata sampled in both October 1999 and 2000 (Fig. 2); however, their concentrations were low, $<1 \text{ ind. m}^{-3}$, in strata deeper than 1400 m (Fig. 2). Between 200 and 1400 m, concentrations of dormant C5s were qualitatively uniform, except at the Santa Barbara Basin. It is not possible to test vertical distributions for uniformity using the Kolmogorov–Smirnov test or χ^2 tests, because net sampling violates the assumption of random sampling (Venrick 1986). However, the broad vertical distribution of dormant C5s was evident in their high semi-quartile ranges of depth (Fig. 2; October 1999: $464 \pm 206 \text{ m}$; October 2000: $358 \pm 186 \text{ m}$; $\bar{x} \pm SD$ of all stations except the Santa Barbara Basin). In contrast, the vertical distribution of dormant C5s at the Santa Barbara Basin was characterized by a very high concentration in a single stratum in October 1999 and 2000. In October 1999, the highest concentration of C5s observed was in the deepest stratum sampled, 509 to 542 m (Fig. 2). In October 2000, the maximum concentration of C5s was just above the sill depth (475 m), in the 444 to 470 m depth stratum (Fig. 2). Maximum concentrations of dormant C5s were also observed in the deepest strata in the

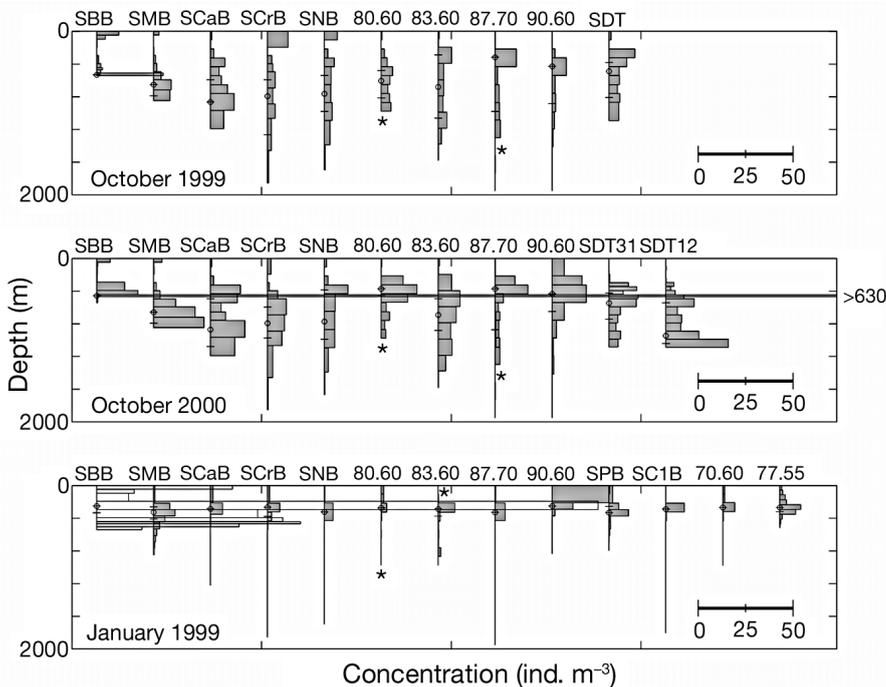


Fig. 2. *Calanus pacificus*. Vertical distributions of Stage 5 copepodids (C5). Abscissa scale within each panel is indicated by a scale bar. Vertical lines indicate maximum sampling depth. Circles indicate median depth of C5s $<200 \text{ m}$, and horizontal lines indicate semi-quartile ranges. Missing samples are marked with an asterisk. Basins sampled were Santa Barbara Basin (SBB), Santa Monica Basin (SMB), Santa Cruz Basin (SCrB), San Nicholas Basin (SNB), Santa Catalina Basin (SCaB), San Pedro Basin (SPB), and San Clemente Basin (SCIB). Non-basin stations sampled included San Diego Trough (SDT) and numbered stations. Strata of high concentration are plotted behind other profiles

pling was coarse, a bimodal distribution of C5s, with very low concentrations between about 100 and 300 m, was observed at most stations (Fig. 2). The percentage of C5s occupying the surface mode was low and variable (1999: $9.6 \pm 14.1\%$ of total abundance;

Santa Monica Basin, the second shallowest basin sampled. In the non-basin stations, higher C5 concentrations near the shallow end of the deep mode were more typical (e.g. 87.70 and 90.60 in 1999; 80.60, 87.70, and 90.60 in 2000).

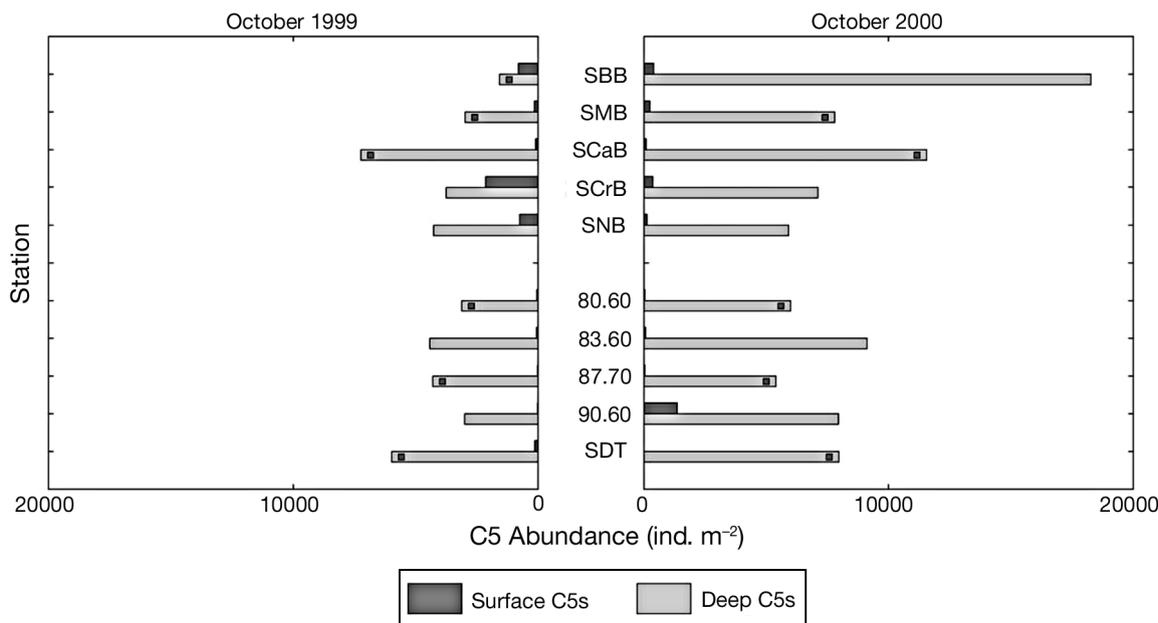


Fig. 3. *Calanus pacificus*. Abundance of surface (less than ca. 200 m) and deep (greater than ca. 200 m) C5s in October of 1999 and 2000. Stations at which C5 abundance may be underestimated are labeled with a gray square

The abundance of dormant C5s was compared across station types (basin and non-basin) and years in October of 1999 and 2000 (Fig. 3). The abundance of deep-dwelling C5s was different in the 2 yr (1999: $4.1 \pm 1.6 \times 10^3$ ind. m^{-2} ; 2000: $8.7 \pm 3.8 \times 10^3$ ind. m^{-2} ; $\bar{x} \pm SD$), while there was no significant difference in abundance between the 2 types of stations (basin: $7.0 \pm 4.9 \times 10^3$ ind. m^{-2} ; non-basin: $5.7 \pm 2.1 \times 10^3$ ind. m^{-2} ; $\bar{x} \pm SD$) and no significant interaction between years and station type (Table 3). This result must be qualified because the abundance of deep-dwelling C5s may be underestimated at several stations (marked with squares in Fig. 3) due to loss of a sample or to limitations in sampling depth. Underestimation is probably highest at stations that have relatively high copepod concentrations in their deepest strata.

The separation of surface and deep C5s observed in October 1999 and 2000 was not distinct in January 1999. In January, deep-dwelling C5s were in shallower water, mainly above 400 m, and the mean semi-quartile range for C5s below 200 m was narrower than in October (43 ± 53 m; $\bar{x} \pm SD$). Adult stages extended into deeper water (300 to 400 m) than in October. C5s made up a lower percentage of the *Calanus pacificus* enumerated in January 1999 than in October, both in deep water and throughout the water column (Table 4). In January 1999, the abundance of C5s throughout the water column was similar among most sta-

tions, except the Santa Barbara Basin, where C5 abundance was much greater (5.2×10^4 ind. m^{-2} , compared to $1.9 \pm 2.0 \times 10^3$ ind. m^{-2} ; $\bar{x} \pm SD$, at other stations).

California Undercurrent water was present at all stations within the continental borderlands of the SCB (i.e. all basin stations and the San Diego Trough) at all dates sampled. Outside the continental borderlands, water properties indicating undercurrent water were weak or absent. In October of 1999 and 2000, dormant C5s were present at a broad range of densities, mainly

Table 3. Two-way ANOVA with replicates ($n = 5$) comparing the mean abundance of *Calanus pacificus* C5s at 2 types of stations (basin and open water) in October of 1999 and 2000

Source	df	F	p
Type	1	2.395	0.14
Year	1	14.515	0.002
Type \times Year	1	2.217	0.16
Error	16		

Table 4. Student's *t*-test comparing developmental stage distributions in January and October. Tests were performed on arcsine-transformed C5/(C4 to C6) abundance proportions. Means are reported as back-transformed values. n_{Jan} , n_{Oct} : number of observations being compared between January and October

Depth category	Jan \bar{x}	Oct \bar{x}	n_{Jan} , n_{Oct}	<i>t</i>	p
Deep	76.3%	99.7%	13, 20	10.239	<0.0001
Water column	61.2%	92.2%	13, 20	5.201	<0.0001

below the vertical center of the undercurrent at $\sigma_\theta = 26.5$, and their distribution relative to density was not qualitatively different between stations inside and outside the continental borderlands. The mean depth of the undercurrent core was 190 m. In January, dormant C5s were primarily found within the density range of the undercurrent, although low concentrations were also present in deeper water at several stations.

DISCUSSION

In the 'canonical' view of dormancy in oceanic copepods, dormant stages accumulate during part of the year until all or nearly all of the population is represented by dormant individuals. However, deviations from this pattern occur in many regions, particularly in populations living at the extremes of their geographical range (Conover 1988). Although part of the *Calanus pacificus* population remains active year-round in the waters off Southern California (Fleminger 1985), seasonal time-series studies in the San Diego Trough and Santa Barbara Basin have found that nearly the entire population, as represented by late copepodid stages, is dormant in October (Osgood & Checkley 1997b, Johnson & Checkley 2004). The present study suggests that this pattern holds throughout the region off Southern California, as the great majority of late copepodid stages were represented by C5s in deep water in October. Copepod dormancy is usually associated with regions of high seasonal environmental variability (Dahms 1995); however, seasonal variability off Southern California is relatively weak, and inter-annual variability is strong (Mullin 1986). Nevertheless, most of the *C. pacificus* population appears to become dormant for part of the year in this region, similar to *C. pacificus* near the northern end of its range in Dabob Bay, Washington, USA (Osgood & Frost 1994).

At the San Diego Trough, the distribution of dormant C5s deepens and broadens from June until October, and then shoals and narrows from October through January (Johnson & Checkley 2004). Similar seasonal shifts in the vertical distribution of dormant copepods, from a deep, broad distribution in October to a shallower, narrow distribution in January, were also observed in the present study throughout the region off Southern California. The depths occupied by dormant C5s in October remove most of the dormant population from equatorward transport in the California Current, which extends to depths of about 300 m outside of the SCB (Lynn & Simpson 1987), and expose shallower C5s in the SCB to poleward transport in the California Undercurrent. Undercurrent flow is strong in the summer and fall, the season of dormancy, and although the core of the undercurrent is narrow, lower-

velocity poleward flow in the California Undercurrent can extend 100 to 150 km offshore (Lynn & Simpson 1990). The broad depth distribution of C5s in October may reflect a trade-off between the benefit of poleward transport for population retention and the cost of higher metabolic and visual predation rates in the warm (8 to 9°C), relatively shallow undercurrent. Residence at the depth of the California Undercurrent may also increase the risk of offshore transport in eddies, which would remove copepods from productive coastal upwelling zones (Simpson & Lynn 1990, Chereskin et al. 2000, Collins et al. 2000). Below the undercurrent, mean velocities are close to zero (Lynn & Simpson 1990, Hickey 1992, Collins et al. 2000); therefore residence in deeper water would have a similar effect on retention of *Calanus pacificus* in the California Current System as residence in deep basins.

The similarity in the vertical distributions of dormant C5s across stations in a given cruise or month, regardless of the presence of the undercurrent, suggests similar depth-keeping behavior across the region. The shift from deeper to shallower depths between October and January implies that copepods probably do not track depths where they are neutrally buoyant, as set by body composition and, particularly, wax ester content (Visser & Jónasdóttir 1999), since their depth distribution shoals during late dormancy when their wax ester content is expected to decrease resulting in increased density. However, alternate behaviors that copepods may use to control their depth during dormancy remain to be determined.

No difference was detected in the abundance of dormant *Calanus pacificus* in basins and deep, non-basin stations in October of 1999 and 2000, perhaps because near-bottom copepod abundance was not estimated. A combination of deeper net sampling and near-bottom sampling with alternate sampling gear, such as video and water-collection gear mounted on a remotely operated vehicle, would be required to resolve this question (Hirche et al. 2006). Sameoto & Herman (1990) and Osgood & Checkley (1997b) suggested that dormant copepods become aggregated in deep basins if they descend from water advected over the basin. This aggregation mechanism requires that the depths of dormant copepods be greater than the basin sill depth. In October of 1999 and 2000, most dormant C5s in open water off Southern California were observed between 200 and 1400 m. At the Santa Barbara Basin, 77% of this depth range is below the sill depth (Table 2), the highest percentage of any basin examined. At the Santa Monica Basin, which shares with San Pedro Basin, the second shallowest sill depth of the SCB basins (Emery 1960), 55% of the depth range of dormant copepods is below the sill depth, and at Santa Catalina, Santa Cruz, and San Nicolas Basins, a

third or less of this range is below the sill depth. These estimates are seasonal maxima, as vertical distributions of dormant *C. pacificus* are deepest in October in this region (Johnson & Checkley 2004). Thus, most basins in this region have relatively little potential to trap dormant *C. pacificus*.

The difference between dormant C5 mean abundance on the 2 October dates sampled is consistent with strong interannual variability in *Calanus pacificus* abundance at the surface in this region (Mullin 1998, Rebstock 2002). The difference in abundance between the 2 yr, approximately a factor of 2, may represent either a difference in the maximum seasonal abundance of dormant *C. pacificus* or in the timing of the seasonal abundance peak of dormant copepodids. The high abundance of the dormant phase of the population in deep water in fall implies that seasonal variation in *C. pacificus* abundance is overestimated in samples collected by the CalCOFI program, a long-term monitoring program that has sampled zooplankton in the upper 140 or 210 m of the water column since 1951. *C. pacificus* is a biomass dominant in the California Current System, and therefore estimates of seasonal variation in zooplankton biomass must also be overestimated. Vertical migration associated with dormancy, as well as the possible changes in its dormancy timing, must be considered in studies of long-term variability in both *Calanus* abundance and zooplankton biomass that use the CalCOFI data (e.g. Roemmich & McGowan 1995, Mullin 1998, Rebstock 2002).

Comparison of dormant C5 abundance in the Santa Barbara Basin with previous studies indicates even higher interannual variability than implied by the present study (Alldredge et al. 1984, Osgood & Checkley 1997b). High interannual variability in dormant C5s at the Santa Barbara Basin may reflect either region-wide levels of variability or processes unique to the Santa Barbara Basin. Interannual differences in the seasonal dynamics of dormant *Calanus pacificus* in the basin (Osgood & Checkley 1997b, present study) suggest that the latter may be true. In addition to the Santa Barbara Basin's unique, shallow morphology, it is also subject to relatively unpredictable flushing events and to climatically induced shifts in circulation (Bograd et al. 2002, Winant et al. 2003). Oxygen concentrations in the deep Santa Barbara Basin, an indicator of basin flushing, were different in October 1999 and 2000. In 2000, oxygen concentrations were very low, 0.01 ml l^{-1} or less, below 500 m (Scripps Institution of Oceanography 2001), and copepods were absent from the deepest strata sampled. In 1999, elevated oxygen concentrations in deep water (0.16 ml l^{-1} at 569 m) indicated that the basin had recently been flushed (Scripps Institution of Oceanography 2000), and maximal concentrations of C5s were observed in the deepest MOCNESS

stratum (513 to 546 m). These observations support Osgood & Checkley's (1997b) hypothesis that dormant copepods may be forced out of the deep Santa Barbara Basin by very low oxygen concentrations; if they move above the sill depth, they would be dispersed from the basin. Irregular basin flushing and resulting shifts in deep-water conditions may lead to significant interannual differences in the abundance of *C. pacificus* that can be retained in the Santa Barbara Basin throughout the dormant season.

CONCLUSION

Osgood & Checkley (1997a) proposed that the Santa Barbara Basin could serve as a significant point source of *Calanus pacificus* emerging from dormancy and seeding population growth in surface waters of the SCB. The results of the present study suggest that, with the exception of the Santa Barbara Basin, deep basins of the SCB have little effect on the concentration and abundance of the dormant copepods residing in them, and that seasonal dynamics of dormant copepods are similar in basins and in deep water outside of basins. Migration to deep water associated with dormancy moves copepods out of equatorward flow at the surface into low-velocity water either inside or outside basins or into poleward flow in the California Undercurrent. Dormant *C. pacificus* are widespread and abundant in deep water throughout the region sampled; therefore, non-point sources of dormant *C. pacificus* are probably numerically dominant in seeding surface waters in the California Current System.

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